

**An ethological study of *Dichragenia pulchricoma* (Arnold)
(Hymenoptera: Pompilidae), a southern African spider-hunting
wasp which builds a turreted, subterranean nest.**

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INTRODUCTION

It is estimated that at present between five hundred and six hundred species of the family Pompilidae have been described from the Ethiopian Region excluding Madagascar. As far as can be ascertained, not a single African species has been studied with respect to its ethology; indeed, the only published biological information pertaining to these nearly six hundred species appears to consist of about half a dozen prey records involving as many species of wasps, a list of species visiting a plant attractive to Hymenoptera, and a few other fragments in which the identity of the wasp concerned is not clearly stated.

Whatever the causes for this shocking hiatus in our knowledge of the African Pompilidae, it is patently obvious that a study of their biology is a potentially most rewarding field of endeavour, where virtually any observations made and recorded will be new.

An inherent difficulty associated with the gathering and recording of information of this nature, however, is the unpredictability in terms of time and place of the opportunity of observing this or that species doing something. The approach towards the study must be an opportunistic one in which whatever presents itself is followed up—an approach practised by the present authors. Thus, though the authors' curiosity had been aroused by the discovery on rare occasions in previous years of the nest turrets of *Dichragenia pulchricoma* (Arnold), the present study of the ethology of this wasp was not so much the outcome of a prior decision to investigate this species as of an unexpected opportunity which presented itself. This opportunity of making a relatively detailed study of what appeared to be a most unusual wasp arose from the chance discovery, during routine collecting in 1972, of two nesting sites, conveniently near Grahamstown, where this species occurred in large numbers.

As an understanding of the basic form of the nest of *D. pulchricoma* is required to appreciate fully not only the import of various statements made but also the relevance of techniques listed in the initial sections of this paper and as a detailed description of the nest follows only later, a brief statement concerning the nature of the latter is given at this juncture.

The nest of *D. pulchricoma* consists of two main sections—a subterranean portion consisting of a vertical burrow or shaft with at or near its end a variable number of cells and an aerial portion consisting of a mud turret of definite form surmounting the burrow entrance which latter is situated at ground level.

TECHNIQUES USED IN EXAMINING NESTS

After a nest turret had been located in the field, it was, if possible, covered with an inverted drinking glass, the aim being to capture the female nest-building wasp should she be in the nest at the time. Capture and subsequent examination of the female is essential, if verification of the species is required. The behaviour of the wasp is such that, having emerged from the nest on an outward-bound flight, it will only return to the nest after this has been carried out. Thus, if the wasp is in its burrow when a glass is placed over its turret, the wasp on emerging will be effectively trapped within the glass and can then be collected easily by introducing some ethyl-acetate impregnated cotton wool beneath the glass. A watch may be maintained at the covered turret until the wasp appears. If the wasp was away, when the glass was placed in position, the latter may be removed long enough to allow the wasp into its nest or an attempt may be made to capture the wasp then and there with a net. Sometimes the wasp remains in the nest until the turret is sprayed as described below, when it emerges very rapidly, and quick action must be taken to prevent its escape.

If, as in the present study, it is wished to preserve the nest turret which is of an extremely delicate and fragile nature, it is essential to impregnate the dried mud pellets of which it is made with a penetrating fluid which on drying hardens the individual pellets and glues

neighbouring pellets together. In the present study an aerosol clear lacquer was found most effective. The lacquer was sprayed fairly liberally onto the turret and particularly onto the ground for a distance of about three to five centimetres around its base. After allowing the spray to dry (about $\frac{1}{4}$ hour in hot sunshine) the sprayed ground around the base of the turret was undercut with a strong penknife. The so-produced consolidated earthen disc bearing the turret itself was then lifted intact and placed on cotton wool in a small unit-tray in which it was readily incorporated into the collection.

As soon as the turret had been removed, the top of the vertical shaft then exposed was cleared of any material that might have blocked it, when the former was undercut and lifted. Flour was then blown down the shaft coating the walls with a white tracer which was indispensable in the subsequent excavation. In the present investigation a plastic mustard-dispenser as seen on the tables of some restaurants was used—the tip of the nozzle fitted to the screw-off top was directed into the shaft-opening and the container was then squeezed to blow out the flour.

In order to expose and draw the vertical shaft and the cells at or near its end, it was essential to excavate the nest from the side. A pit about fifteen centimetres deep and at least as long and wide was, therefore, dug to one side of the assumed position of the nest, the nearer side of the pit being about seven centimetres away from the shaft opening. As the ground was usually extremely hard, a geologist's pick was used to make this initial excavation. Working from the pit towards the nest, the ground was then carefully broken away using initially a cold chisel and club-hammer, later the point of a penknife. Final exposure of the shaft (marked with flour) and of the cells (if sealed not marked with flour) called for precise and careful work.

A plan was drawn and measurements of the nest taken as the latter was exposed, notes were taken of the nature of the cells, the prey and the wasp young. Prey and wasp young of each cell were individually collected in labelled glass vials or gelatin capsules and kept alive for subsequent closer examination.

SYSTEMATIC AND TAXONOMIC CONSIDERATIONS

In the key to genera and species of the tribe Macromerini (as subfamily Macromerinae) published by Arnold (1934: 289—95), the present species runs down easily to *Pseudagenia pulchricoma* Arnold, with the description of which (1934: 337—9) it agrees perfectly. No authoritatively determined specimens were available to confirm the identification but comparison with specimens of the subspecies *sordida* Arnold from Lesotho, identified as such by Arnold himself, supported the determination, allowance being made for the stated differences.

The present specimens are characteristically coloured: the greater part of the head and thorax (including the pronotum) is black, the wings are pale fuscous, while the abdomen is mostly ferruginous as are the legs with the exception of the coxae. In the female, the clypeus and antennae are ferruginous (the latter becoming gradually darker from the third or fourth joint onwards), the face, pro-mesonotum and scutellum have a pale greyish golden pubescence, while the second to fifth tergites are marked medially with black maculae which do not reach the posterior margins of the segments but which together give the impression of a somewhat diffuse, wide, median streak on the dorsum of the abdomen. This black streak on the otherwise ferruginous dorsum of the abdomen, taken in conjunction with the black thorax and fuscous wings readily identifies the wasp in the field. The male is similarly coloured but lacks the black streak on the abdomen.

Since the time of Arnold's revision of the Pompilidae of the Ethiopian Region (1932—7), the very large cosmopolitan genus *Pseudagenia* Kohl, 1884 (= *Auplopus* Spinola, 1841) has been split up into a number of smaller genera.

Banks (1934) in his account of the Psammocharidae of the Philippines removed from *Pseudagenia* (*sensu lato*) one new subgenus and seven new genera, not all of which have been recognized by subsequent workers.

The present species, *pulchricoma* Arnold, would, according to the generic key given by Banks (1934: 39—40) be referable to the genus *Phanagenia* Banks (1933: 18). This genus, recognized as valid by subsequent workers, was erected “for certain American forms possessing spines on the underside of the last tarsal joint” (Banks, 1934: 78). The generic description (of the female only) of *Phanagenia* (type species: *Phanagenia osceola* Banks, 1933 = *bombycina* (Cresson), 1867) is short, but the characters indicated are all exhibited by the present species, *pulchricoma* Arnold.

In the key to the Nearctic genera of the Macromerini published by Townes (1957: 140) *pulchricoma* Arnold once more runs down to *Phanagenia* Banks, which genus according to Townes differs from *Auplopus* Spinola, 1841 (= *Pseudagenia* Kohl, 1884) and two other genera (*Ageniella* Banks and *Priocnemella* Banks) in the following combination of characters: (1) first tergite with a fine lateral crease that separates off the epipleuron; (2) propodeum without long erect hairs; (3) mentum of female with a brush of about 20 long stout bristles which are not divided into right and left groups; and (4) underside of last tarsal segment of female with preapical bristles.

The present species, *pulchricoma* Arnold, differs in having the mental bristles of the female rather sparse and in having the clypeus of the male simple (clypeus of male with specialized apical margin in *Phanagenia bombycina* (Cresson)). However, the same differences have been accepted as possibly merely specific ones by Townes (1957: 141), when considering the Madagascan *Agenia macula* Saussure as a possible Old World member of the genus *Phanagenia*.

Agenia macula Saussure has also been studied by Haupt who, however, named it as the type-species of *Dichragenia* (1950: 25 and 1957: 14), one of several new Ethiopian genera split off by him from *Pseudagenia* as understood by Arnold. *Dichragenia*, according to Haupt, is represented on the African continent itself by *pulchricoma* Arnold, the subject of this paper.

Without being able to compare the type-species of *Phanagenia* and *Dichragenia*, it is not possible to assess fully the morphological differences between the two, differences which undoubtedly are small.

While the ethology of *Dichragenia macula* (Saussure) is unfortunately unknown, that of *pulchricoma* Arnold differs in important aspects from that of *Phanagenia bombycina* (Cresson) and lends support to generic separation. In the present paper Haupt's view is adopted and the wasp is referred to as *Dichragenia pulchricoma* (Arnold).

Arnold (1934: 337—40) as well as describing *pulchricoma* (*sensu stricto*) from “Southern Rhodesia and British East Africa”, described two subspecies (“races” of Arnold): *sordida* from Harrismith (Orange Free State), Willowmore and Aliwal North (both Cape Province); *laeta* from Umtata (Cape Province), Delareyville (“De la Rey” of Arnold) and Lichtenburg (both Transvaal).

In the Albany Museum collection there are fair-sized series of both these “races”—9 females and 6 males of *sordida*, and 8 females and 15 males of *laeta*, the determinations being by Arnold himself. Unfortunately, all these specimens are from Lesotho, all but one from the same locality, Mamathes; months of capture for both are October—February/March, in quite a number of cases in the same year! From the above it is clear that *sordida* and *laeta* cannot both be considered as subspecies of *pulchricoma*.

Some aspects of the ethology of one species of “a certain group of spider hunters” in Lesotho have been observed by Jacot-Guillarmod (1945: 43). He refers to this species as “the Zimbabwe builder” and from personal discussions in 1972 it emerges that the wasp in question was *sordida*. As far as the information goes, no differences can be found with respect to the ethology of *pulchricoma* (*sensu stricto*) as studied in Grahamstown. This together with

the great general morphological similarity leads to the view that *pulchricoma* and *sordida* are indeed conspecific. On the other hand, despite the fact that *laeta* was more common than *sordida* in Lesotho, it was, unlike the latter, never observed nesting (Jacot-Guillarmod, pers. comm., 1972), leading to the belief that it may well do so in a different ecological situation. This taken in conjunction with the general morphological differences leads to the view that *laeta* is not conspecific with *pulchricoma* but is better regarded as a separate species. This view agrees with that expressed by Arnold in 1961 when, during discussions with Jacot-Guillarmod, his attention was drawn to the fact that *sordida* and *laeta* are sympatric in Lesotho (Jacot-Guillarmod, pers. comm., 1972).

GEOGRAPHIC DISTRIBUTION

Dichragnia pulchricoma (Arnold) appears to enjoy a very wide distribution in Africa. Published locality records indicate a distribution from the equator (Kisumu, Kenya, at the north-eastern extremity of Lake Victoria) to the southern parts of the Cape Province (33°S.), ranging through several major vegetational zones.

In addition to the localities given by Arnold (1934: 339—40)—namely, Rhodesia (where “a common species”), Kisumu (“British East Africa”), Harrismith (Orange Free State), Aliwal North and Willowmore (both Cape Province), the species has been recorded from a number of widely separated localities in Zaire (the former Belgian Congo) by de Saeger (1945: 99) and by Haupt (1957: 15).

The Albany Museum collection contains specimens from Lesotho (Mamathes, Teyateyaneng and Henley’s Dam, Leribe) collected by C. F. Jacot-Guillarmod (October—February) and from the Eastern Cape Province (various localities near Grahamstown). A nest turret, now in the collection, obtained by R. A. Jubb at Kenton-on-Sea, 44 kilometres SSE of Grahamstown, indicates the species’ presence there.

It is probable that the species occurs also in the western part of the Cape Province for a single female associated with a nest turret of typical form and believed to be *D. pulchricoma* was observed but not caught by one of the authors (F.W.G.) at the Olifants River between Klawer and Clanwilliam during October 1967.

LOCALITY AND DESCRIPTION OF NESTING SITES WITH PARTICULAR REFERENCE TO CLIMATE, NATURE OF VEGETATION, SOIL TYPE AND VICINITY OF WATER

Field observations in the present study were centred on Grahamstown (33° 19’ S, 26° 32’ E) in the Albany Division of the Eastern Cape Province of South Africa. The greater part of the field work, including the study of 55 nests was carried out at Hilton, a farm situated about 18 kilometres WNW of Grahamstown; a smaller number of nests (6) was studied at a second farm, Clifton, situated at about the same distance from the town but to the NW; one nest and its builder were studied in the authors’ garden in Grahamstown itself. The greater part of the field work was spread over a period of six weeks from 26.x.1972 to 6.xii.1972; an additional three mornings’ field work was carried out at Hilton later in the summer (9 and 14.ii.1973 and 1.iii.1973).

The Albany Division, situated between the winter and summer rainfall regions, receives rain in moderate amounts throughout the year, the wettest periods being spring and autumn, the driest mid-winter. Grahamstown itself has a mean annual rainfall of 697,2 mm (27,45 inches), however, the farms Hilton and Clifton, for reasons of topography, receive considerably less—at Hilton the mean annual rainfall is in the region of 356—381 mm (14 to 15 inches). During 1972, a drought year, Grahamstown received 532 mm (20,94 inches) and Hilton received only 229 mm (9 inches).

The vegetation of Hilton and Clifton is karroid in nature and consists largely of an open community of small shrubs, few of which are strongly succulent but many of which are xerophytic. *Acacia karroo* forms much of the taller scrub, and grasses have largely been eaten out by stock. In both localities there has been some erosion of the soil resulting in some localized denuded areas.

Nesting sites at both Hilton and Clifton as well as in Grahamstown itself are in low-lying situations (river valleys) in which the soil is derived from the Dwyka Series and is of a reddish-brown clayey nature.

All nests found during the present investigation were built in places where the ground had been disturbed and had been partially or completely denuded of vegetation as a direct or indirect result of Man's activities.

Thus at Hilton, nests were found on the slightly raised edges of a shallow earthen dam; on the raised bank of earth running parallel to a water furrow and derived from the excavation thereof; on the denuded ground on the opposite side of the furrow; on slightly sloping areas denuded of vegetation and topsoil by sheet erosion, and on the sides of small erosion gullies intersecting such bare areas (Plates 1—4). At Clifton nests were found in essentially similar situations; the nest found in Grahamstown was situated on bare earth fringing a vegetable bed.

Mud turrets surmounting the burrow entrances were sometimes found completely exposed in the middle of totally bare areas but were sometimes in somewhat more protected situations such as against small banks or steps in the ground level or next to the base of dwarf shrubs (Plates 5—8).

In all cases the nests were situated in close proximity to temporary sources of water. This water, a result of rain, had collected in muddy pools, erosion gullies, shallow furrows and, in the case of the garden, a concave cabbage leaf.

Similarly the previously mentioned nest turret observed at the Olifants River and believed to be that of *D. pulchricoma* was sited on a fairly steep, bare, sheet-eroded clayey slope situated not far from two water sources—the Olifants River itself, and, closer at hand, muddy pools below a leaking concrete irrigation furrow.

Turrets of nesting *D. pulchricoma* at Mamathes (Lesotho) were reported by Jacot-Guillarmod (pers. comm.) to have been built on denuded patches of black clay near a spring.

GENERAL COMMENTS CONCERNING NESTING AND AN ACCOUNT OF THE BEHAVIOUR ASSOCIATED WITH BURROW EXCAVATION AND TURRET CONSTRUCTION

Dichragenia pulchricoma (Arnold) appears, at least in the localities studied (around Grahamstown), to be an opportunist—emerging in response to rain and nesting during the short period during which standing water, essential for nest construction, is available in pools and puddles. However, it appears as if only a fraction of the total population responds to any one fall of rain, for during summer, that is during the period of October to March, each shower of rain substantial enough to wet the ground and to cause run-off to form puddles in depressions, is followed by a flush of wasps and a spate of nest-building. As the puddles dry up again, the number of wasps observed falls off and nesting ceases. Thus, the potential nesting season is divided up into a number of short nesting bouts by apparently successive waves of wasps; the period between the emergence of the wasps and the completion of their nesting is very short; and, at any one time, virtually all nests being worked upon are at a similar stage of development. Comparison, with respect to stage of development and size, of wasp young present in a number of nests examined on a day soon after the beginning of a nesting bout with young present in other nest samples examined on subsequent days (Fig. 1),

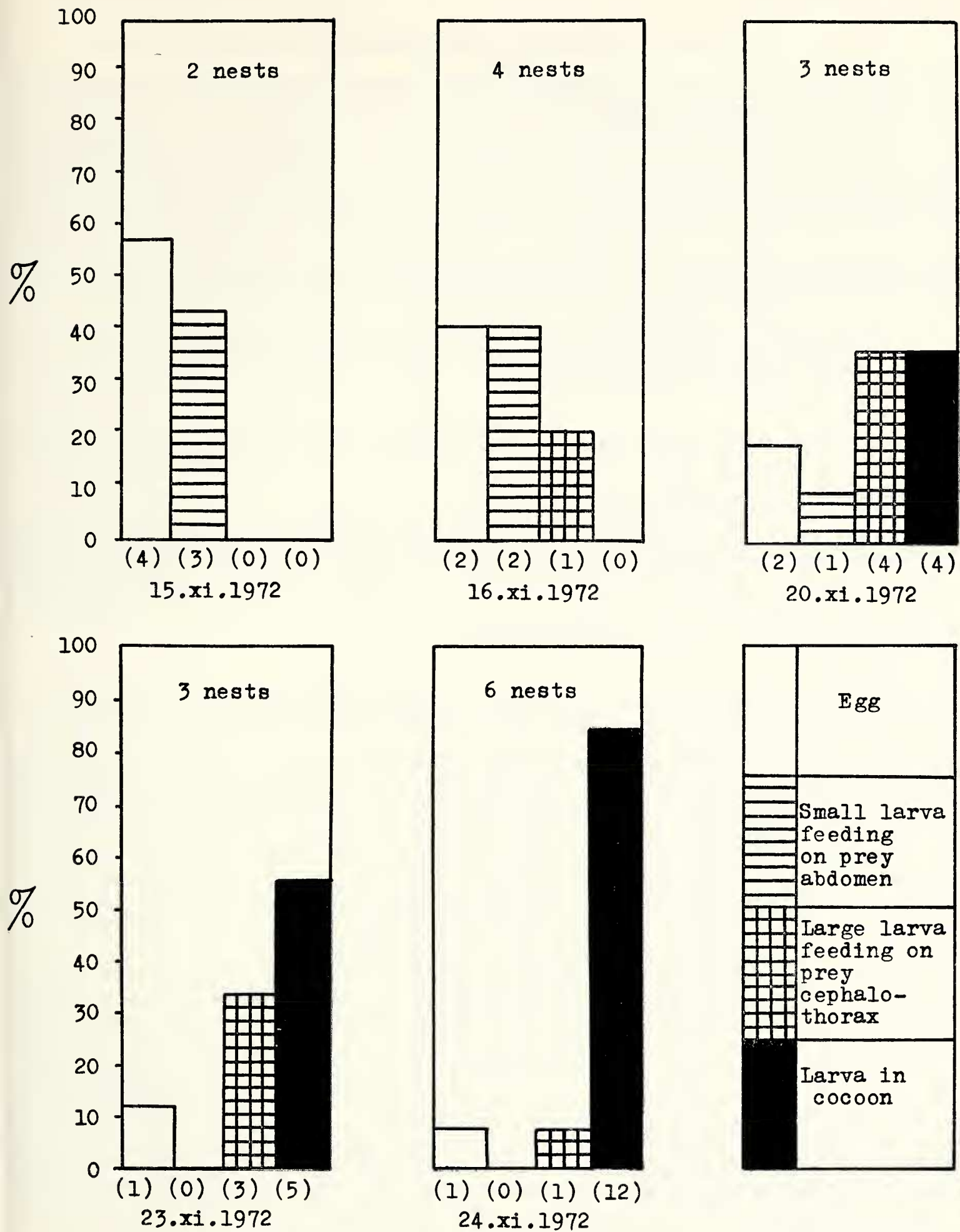


Fig. 1. Composition (expressed as a %) of wasp young (egg, small larva, large larva and larva in cocoon) collected at Hilton during the period 15—24.xi.1972. The actual number of each stage is indicated within brackets.

illustrates not only the synchrony of nesting within any one nesting bout but also the rapidity of development from egg to mature larva.

No evidence was found that might suggest that there was more than one generation of wasps per year. Indeed, in all the nests examined the most advanced young were fully-grown larvae within silken cocoons; no pupae were found. It seems likely that these larvae do not immediately pupate but rather enter a state of diapause in which the rest of the nesting season, the autumn and the dry winter months, are spent and that the stimulus for the breaking of the diapause is at least in part provided by the rains of the following spring and early summer. Presumably, development thereafter is rapid as is the previous development from egg to mature larva.

The behaviour associated with burrow excavation and turret construction consists of a cycle of events which is repeated many times over. Each cycle may be considered to consist of three major activities as indicated below.

(1) *Water carrying*

Flying from the nest under construction to the nearby water source, filling the crop with water and returning to the nest.

(2) *Shaft excavation (sinking) and turret building*

Regurgitation of some of the water onto the earth at the working face of the vertical shaft being sunk, the excavation with the aid of the mandibles of the resultant mud and the moulding thereof into a pellet (building block), the transport of this pellet up the shaft and its addition to the free edge of the turret rising up above the mouth of the shaft. This major activity is repeated a number of times within each cycle.

(3) *Grooming*

Grooming of the head in general and the antennae in particular before setting out to fetch the next crop-full of water—that is, before initiating the next cycle.

It will be seen that the excavation of the subterranean portion of the nest is intimately linked with the building of the turret above ground and that the size of the turret (provided it has not been damaged) provides a clear indication of the extent of the underground workings.

A wasp occupied in nest building in the Grahamstown garden on 16.xii.1972 was observed for a period of 60 minutes. During this time 13 of the above defined cycles were completed. About 12 minutes were devoted to water carrying and about 48 minutes were spent on activities at the nest (shaft excavation and turret building as well as grooming). Within the 60 minutes, 68 mud pellets were formed from excavated materials (derived from the excavation of the vertical shaft) and placed in position on the free edge of the turret.

Similarly, a wasp, observed at Hilton on 1.iii.1973, completed 11 of the above defined cycles in a period of 39 minutes, of which 6 minutes were devoted to water carrying and 33 minutes to activities at the nest. Within the 39 minutes, 52 mud pellets were formed and positioned, resulting in an increase of turret length of between two and three centimetres.

The nests of both these wasps were situated close to the water source being utilised—the former about 7 metres distant, the latter 2,3 metres (Plate 2). When fetching water *D. pulchricoma* alights near the water's edge, walks the last few centimetres and drinks from the edge of the puddle. Similarly, when returning to the nest, she commonly alights 15 to 30 centimetres away from the turret and walks the rest of the way but occasionally alights much closer to the turret or even lands upon the latter. Flights to and from the water is generally direct and rapid.

On returning to the turret the wasp enters it head first. Shortly thereafter her head reappears at the free edge of the turret holding between her mandibles a glistening pellet of

very wet mud. This is placed in position on the free edge of the turret by the wasp which builds from within the latter, only her head and prothorax emerging. Having positioned the pellet, the head disappears again only to reappear a short while later with the next pellet. The number of pellets formed by the removal of material from the shaft face and positioned on the turret edge varies from 2 to 8 (with an average of 5) per single water load. Though it could not be observed, it is believed that the very wet mud pellet, in addition to being held by the mandibles, is supported from below by the stiff mental bristles which would act in the manner of a pitchfork.

The last pellet of a batch having been formed and positioned, the wasp grooms thoroughly before departing for more water. This grooming, in which particular attention is given to the antennae, may take place in the turret entrance or on the ground next to it.

Nest construction appears to take place during the hottest period of the day—the building activities described were observed between about 10.40 a.m. and 1.30 p.m. although already begun before and continued after these times. Building is carried out only in strong sunshine; when the sun is obscured by clouds work ceases.

During the period of nest construction, when the females are frequent visitors to the puddles and pools where they obtain their water, their presence or absence at such water sources is a reliable guide as to whether nesting is taking place in any given locality. Males, which in the present study were never observed at the actual nesting sites, are found near these watering places. At Hilton, males, if not on the wing, could frequently be flushed from tussocks of coarse grass and sedges fringing pools visited by the females (Plate 2 and 4). These circumstances suggest that mating may take place at the pools, when the females come to these for water.

DESCRIPTION OF THE NEST TURRET

The turret built above the entrance to the subterranean part of the nest is more or less circular in cross section, is of variable diameter along its length and is curved in at least the vertical plane. For any given nest the extreme base or foundation of the turret wall is at a fixed distance from the nearest edge of the vertical shaft opening and is obviously a function of the size of the wasp builder. Therefore, any deviation from the circular in the shape of the shaft opening is mirrored in the shape of the turret foundation and large wasps build turrets of greater bore than do small ones. Generally the internal diameter of the turret at its base is about three times that of the vertical shaft, with the consequence that there is incorporated within the structure of the nest a platform-like disc of the ground surface, bounded at its circumference by the turret walls and pierced at its centre by the entrance to the vertical shaft. As the turret rises the bore generally increases slightly, then decreases again to form basally a weakly developed bulb-shaped bulge beyond which the bore continues to decrease gradually towards the distal turret opening. For 42 turrets measured, the outside diameter at the foundation varied from 14 mm to 26 mm, the most common diameter was 19 mm and the average 20,5 mm; the outside diameter at the distal end of 24 of these turrets (those which were considered complete or near-complete) varied from 10 mm to 18 mm, the most common diameter was 13 mm and the average 13,5 mm.

Turrets generally start off subvertically but almost immediately begin to curve over to one side to form an arch over the ground and to bring the turret entrance down close to the latter. If the turret is lengthened by the addition of further excavated material, it then levels out horizontally and runs parallel to the ground to which it may or may not be attached. This section of the turret may curve laterally or become sinuous. Only one of a total of 64 turrets studied did not initially rise up above the ground—instead, for its entire length it ran along the ground which latter formed the floor of the domed runway.

The height above the ground attained by the top of the turret arch was found to vary considerably in the 25 turrets suitable for measuring—from 13 mm to 65 mm; 50% of these turrets fell in the 24—27 mm range and the average height of all 25 turrets was 28 mm.

The length (measured along the outside of the curve) of 15 intact turrets belonging to nests containing at least one cell varied from 42 mm to 140 mm; 50% of these turrets fell in the 60—80 mm range and the average length of all 15 turrets was 77 mm.

The pellets used as building bricks in turret construction are roughly elongate-oval in shape with a slight constriction at the middle of the long axis and approximate best to the form of a two-seeded peanut pod. Each pellet is laid with its long axis orientated across the long axis of the turret. The pellets vary somewhat in size between different turrets and sometimes also within different sections of any one turret. This variation is probably due not only to differing wasp sizes but also to varying physical conditions of the soil. The pellets forming the walls of the basal bulge are generally closely packed and leave but few interstices of small size between them. Beyond the bulge the pellets tend to be more loosely laid and leave between them large spaces giving this section of the turret a lacy appearance. No smoothing or plastering of the bore of the turret is practised by the wasp and the individual pellets are as distinct on the inside surface of the turret walls as on the outside.

A well-built turret of typical form surmounting underground workings consisting of a single, sealed cell situated at the end of a 118 mm long vertical shaft (Fig. 2) was photographed in the field at Hilton (23.xi.1972) and is shown in Plate 6. Its dimensions are: outside diameters at base and at end 18 and 12 mm respectively; height of top of arch above ground 29 mm; total length 70 mm.

The turrets have little resistance to wetting and even a very light shower of rain will cause the pellets to melt and the turret to collapse. A total of 22 rain-damaged turrets were found at various times during the season, 20 of which had been subject to subsequent building activity. A new turret is frequently built out from what remains intact of the original one but is often inferior in construction and size to the latter and usually consists of little more than a crudely-added, narrow, lacy tunnel akin to the narrow distal portion of a normal extended turret. In one instance, where the original turret had only reached half the height of the basal bulge before being damaged by rain, the replacement of very inferior construction was built within the walls of the old structure.

Thus it is believed that the additions built subsequent to rain damage are not repairs but rather a continuation of normal building activity which would have taken place in any case at the free distal end of the turret but which activity has been shifted back in position to a new distal end—the point beyond which the original structure was destroyed. The inferior quality of the additions is thereby explained: what is more difficult to explain, however, is an instance in which a turret replacing a large collapsed one was of normal form though rather smaller than average.

The function of the turret is unclear. It seems unlikely that it would prove much of a deterrent to a determined parasite or even a casual one—it certainly did not prevent five separate instances of nest parasitism by leaf-cutting Megachilidae, though it must be stated that, perhaps significantly, in all five cases the turrets were not very extensive and consisted only of that portion up to the top of the arch. As already stated, the turret is destroyed by even a light shower but it is possible that its collapse may be of advantage to the wasp in that the debris plugs the entrance to the vertical shaft preventing flooding of the underground portion of the nest. Finally it may be of some advantage to the wasp that on coming up the vertical shaft it does not immediately emerge into the open but rather does so only after passing through the turret through the walls of which it is able to see the surroundings.

DESCRIPTION OF THE SUBTERRANEAN BURROW AND AN ACCOUNT OF THE SEQUENCE OF CELL CONSTRUCTION AND PROVISIONING

A total of sixty nests in various stages of construction was excavated during the present study. In Table I, the underground workings of these nests are grouped into nine categories according to the number of cells associated with each nest.

The subterranean portion of the nest consists of a vertical or near-vertical shaft near the lower end of which are situated a variable number of cells. The vertical shafts of the 42 nests included in categories B—I of Table I (i.e. those shafts which were complete as indicated by the presence near their ends of at least one cell) penetrated into the ground to depths ranging from 55 mm to 180 mm, with an average penetration of 113 mm. Of the total of these 42 shafts, 76% were between 90 mm and 130 mm deep (long) and with this latter category of shafts was associated 71% of the total of 108 cells. The bore of the vertical shafts varied from 5 mm (a single abandoned shaft) to 11 mm (a single shaft) with 53 of the total of 60 shafts (i.e., 88%) having a bore of between 6,5 mm and 8,0 mm.

Table I. Analysis of the form of the underground workings of 60 nests of *Dichragnia pulchricoma* (Arnold) excavated near Grahamstown (26.x.1972–14.ii.1973).

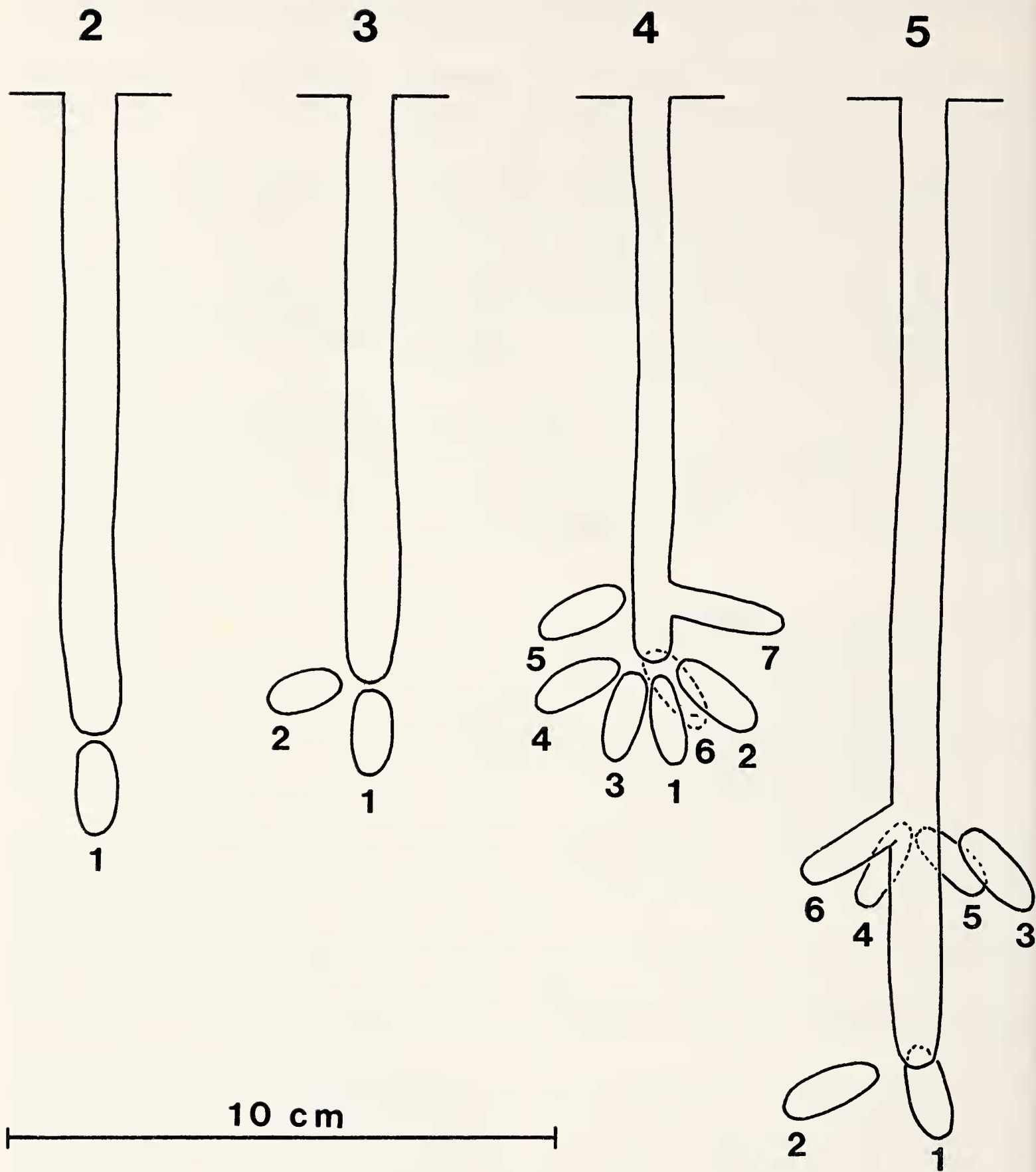
Category	Description of underground workings	Number of nests
A	Shaft with no cells	18
B	Shaft with 1 cell (unprovisioned)	12
C	Shaft with 1 cell (provisioned)	6
D	Shaft with 2 cells (at least 1 provisioned)	6+(2)
E	Shaft with 3 cells (at least 2 provisioned)	5
F	Shaft with 4 cells (at least 3 provisioned)	3
G	Shaft with 5 cells (at least 4 provisioned)	2
H	Shaft with 6 cells (at least 5 provisioned)	4+(1)
I	Shaft with 7 cells (at least 6 provisioned)	1

TOTAL: 60

NOTE: Figures in brackets () pertain to three nests in which for some unknown reason more than 1 cell was unprovisioned—in the former instance two nests each containing 2 cells, neither provisioned, in the latter instance one nest of 6 cells, only four of which were provisioned.

The cells which vary in length from 14 to 19 mm are formed by the sealing off by means of earthen plugs of the distal portion of short (15–25 mm), usually downwardly-inclined sids shafts which branch off from the vertical shaft at or near its terminal (bottom) end. These side shafts (and therefore also the cells) are excavated at roughly a common depth and are arranged around the end of the vertical shaft in a more or less radiating pattern (like the spokes of a horizontally orientated cart wheel). A cell may, however, lie directly beneath the end of the vertical shaft and may represent the sealed off original terminal portion thereof. (Figs. 2–4.)

In one nest with an exceptionally long vertical shaft, cells were found to have been



Figs. 2—5. Plans of the underground workings of four nests of *Dichragena pulchricoma* (Arnold) excavated at Hilton during November, 1972, showing various degrees of complexity and also the sequence of cell construction and provisioning. For details of the condition of the prey spider and of the developmental stage of the wasp young within each cell see Table II.

constructed at two distinct levels—two from the end of the vertical shaft 180 mm below the surface of the ground, and a group of four radiating out from the shaft at a point 130 mm below the surface. (Fig. 5.)

The earthen plug between cell and vertical shaft is flush with the wall of the latter and once in position leaves little indication of the proximal part of the side shaft.

One cell at a time is excavated and as a rule only a single open cell is found at any one time in any one nest. As soon as the cell has been provisioned and oviposition has occurred, it is sealed, after which work commences on a second cell. It was not established where the earth utilized for plugging the cell comes from, but as it does not differ in colour or other appearance from the earth through which the vertical shaft passes, it is believed that it is obtained from within the nest. Possibly the earth is quarried near the end of the vertical shaft at a point close to the cell being closed, and possibly this quarry may subsequently form a convenient starting point for the excavation of the next cell.

The sequence of cell construction and provisioning in multicellular nests may readily be established by virtue of the degree of development attained, at the time of examination, by the wasp young within each of several cells. Clearly, the most informative nest in this respect is one which is still being worked upon by the adult female and which shows a wide range of cell conditions—from a newly excavated, open, and as yet unprovisioned cell to one (but preferably not more than one) containing a mature larva within a silken cocoon.

Figs. 2, 3 and 4 show plans of the underground workings of three progressively more complex nests in which is indicated the sequence of cell construction, as inferred from the wasp young within them. Fig. 5, pertaining to an already mentioned nest, shows an unusual nest plan but the typical sequence of cell construction. Table II shows the condition of the provision (prey spider) and the developmental stage of the wasp young found within each of the cells of these four nests.

In those nests in which it was present, the cell situated immediately beneath the end of the vertical shaft was found to have been the first to be constructed and provisioned. No particular order of construction could be established for the cells radiating out around the end of the vertical shaft but, in those nests in which these cells were numerous, a tendency was noted for later cells to be constructed at a level slightly above initial ones without, however, altering the general clumped arrangement of the cells. In the underground workings shown in Fig. 5 the marked separation between the initial (lower) two cells and the later (upper) four is seen as the consequence solely of the excessively and abnormally long vertical shaft and the abandonment of the lower level after the construction of only two cells there in favour of the more normal depth for cell construction.

IDENTIFICATION, COMPOSITION AND PHYSICAL CONDITION OF THE PREY USED FOR PROVISIONING THE CELLS

From the 72 provisioned cells of *D. pulchricoma* excavated during the present study 38 identifiable prey spiders were obtained. These spiders ranged in condition from some individuals on which feeding by the wasp young had not yet commenced to others which had had the entire abdomen and much of the cephalothorax consumed. The prey spiders of the remaining 34 cells had been completely devoured with the exception of the cheliceral fangs which were always left uneaten by the wasp larvae. With the addition of one specimen taken from a wasp in the act of transporting it to its nest, a total of 39 prey spiders was available for examination. These were identified as follows:

Lycosidae

21 specimens (15 females, 5 males and one specimen of indeterminable sex) (One female, a subadult)

Pisauridae

Euphrosthops sp. 12 specimens (9 females and 3 males) (One female, a subadult)

Sparassidae (formerly included in Clubionidae)

Olios sp. 3 specimens (2 females and 1 male)

Pseudomicrommata vittigerum (Simon) 2 specimens (both females)

Salticidae (= Attidae)

1 specimen (a female)

Immediately apparent from the above prey identifications is the preponderance of adult spiders over subadults, females over males, and members of the Lycosidae over those of other families.

While a nest of two or more provisioned cells may contain prey spiders of one family only, it more frequently contains representatives of more than one family. Thus individual nests were found that were provisioned with Lycosidae and Sparassidae, Lycosidae and Pisauridae, Pisauridae and Sparassidae, and Pisauridae and Salticidae.

The four spider families involved are all composed of strongly built, fast moving, wandering and predaceous ground-living forms which stalk and run down their prey on foot.

Of the total of 39 prey spiders examined, 32 had had all the legs amputated at the coxal-trochantal joint, three each had one leg remaining, and one had two legs remaining. The other three spiders were extensively eaten but between them possessed ten intact coxae from which the distal parts of the leg had been amputated. It is clear that *D. pulchricoma* habitually amputates the legs of its prey: that this amputation is carried out prior to the removal of the prey to the nest was demonstrated by the legless state of the spider, previously mentioned, which was taken from a wasp in the act of transporting it from the point of capture to the nest being provisioned. The pedipalps, by contrast, are not removed.

In size, the total length of the legless spider bodies varied from 8—13 mm, the most common length being 12 mm; the maximum width (measured across the cephalothorax and the leg stumps for all specimens except *Olios* sp. which was measured across the abdomen) varied from 4—6 mm, the most common width (58%) being 5 mm. The "dressed weight" of only one prey spider was established. This specimen, a freshly caught adult female lycosid of average size (total length 11 mm, maximum width 5 mm) and with all the legs amputated weighed 76 mg., somewhat less than double the weight of an average sized female wasp.

MODE OF TRANSPORT OF THE PREY AND THE POSITIONING OF THE LATTER IN THE CELL

Only once was *D. pulchricoma* observed transporting its prey. This was at Hilton (23.xi.1972) where a female wasp was seen carrying a legless female lycosid across open ground in an area in which were located several nest turrets. Progression, with the wasp facing the direction in which it was going, was by a series of short hopping flights, the wasp alighting every few centimetres and running a short distance before trying to take off again.

The spider, held beneath the wasp's body and straddled by the wasp's legs, appeared to be positioned dorsum up and head forward. Unfortunately, the point at which the spider was grasped by the wasp's mandibles was not noted but, on the basis of the otherwise identical mode of prey transport observed in a related wasp species, it is believed to have been the base of one of the chelicerae. The related wasp, "*Pseudagenia*" *spilocephala* Cameron (? another species of *Dichragenia*), whose transport of prey was closely observed on three separate occasions, carried its prey (legless female Lycosidae and *Olios* sp.) beneath it, dorsum up, head forward (as in *D. pulchricoma*), grasped by the base of a chelicera. The actual hunting

Table II. Condition of the provision (prey spider) and stage of development of *Dichragenia pulchricoma* (Arnold) young within each of the cells (listed in order of their construction) of four nests (see Figs 2—5) excavated at Hilton during November 1972.

Nest (Fig. No.)	Cell	Condition of cell	Condition of provision (prey spider)	Stage of development of wasp young
2	1	Sealed	Not fed upon	Egg
3	1	Sealed	Abdomen fed upon	Small larva
	2	Sealed	Not fed upon	Egg
4	1	Sealed	Completely devoured	Larva within silken cocoon
	2	Sealed	Completely devoured	Larva within silken cocoon
	3	Sealed	Completely devoured	Larva within $\frac{1}{2}$ -spun silken cocoon
	4	Sealed	Completely devoured	Very large larva
	5	Sealed	Abdomen fed upon	Small larva
	6	Sealed	Not fed upon	Egg
	7	Open	(None present)	(None present)
5	1	Sealed	Completely devoured	Larva within silken cocoon
	2	Sealed	Completely devoured	Very large larva (15 mm. long)
	3	Sealed	All of abdomen and part of cephalothorax eaten	Medium sized larva (11 mm. long)
	4	Sealed	Abdomen fed upon	Small larva (9 mm. long)
	5	Sealed	Not fed upon	Egg
	6	Open (Wasp builder found in this cell)	(None present)	(None present)

and stinging of the spider by the wasp and the process of leg amputation was not observed in either of the species.

The position in which the prey spider was placed in the cell by *D. pulchricoma* was without exception such that it rested with its ventral surface on the floor of the cell with its head towards that end of the cell nearer the vertical shaft.

OVIPOSITION AND IMMATURE STAGES

Oviposition upon the prey spider takes place only after the latter has been positioned within the cell. Great consistency with regard to orientation and site of attachment of the egg is shown—thus in the observed cases, the egg was without exception found to be securely attached in a somewhat oblique position to the side of the spider's abdomen, near the base of the latter. The morphological anterior end of the egg was uppermost (Figs. 6 and 7). There was no observable preference for either the right or the left side of the spider's abdomen, equal numbers of eggs (and also larvae) being found on both sides.

The young larva on hatching from the egg was found not to move away from the position in which the latter was laid but to commence feeding at the site thus determined for it. The point at which the spider's integument was punctured and where feeding began was on the dorsum of the abdomen to one side of the midline, in the region occupied by the spider's digestive gland (Plate 9). Young larvae engaged in feeding, during which the head was kept firmly applied to the puncture, were observed to engage in pulsating or pumping movements over the entire body. It was found that, when all the fluids had been thus imbibed and the larva had grown stronger, chewing of the harder portions of the abdomen began and the larva's fixed position upon the prey was relinquished. When the abdomen had been completely eaten, the cephalothorax was started upon, beginning at the posterior end and progressing forwards until the whole of the prey including the coxae and the pedipalps but excluding the cheliceral fangs was consumed.

When all the provision has been eaten, the mature larva spins its pale brownish-yellow, partly translucent, parchment-like cocoon which is attached to the cell's walls by fine silken threads. A small opening is left at that end of the cocoon that is situated at the distal end of the cell (i.e., that end away from the vertical shaft) and the head of the mature larva may be seen at this opening at the time cocoon spinning is completed. Thereafter the larva reverses its position within the cocoon thereby bringing the head toward that end through which the adult will emerge. Meconium is released at the cocoon's opening at which the hind end of the larva is now situated, to form a hard, dark-coloured plug sealing the cocoon and, by sticking onto the cell wall, further anchoring the former to the latter.

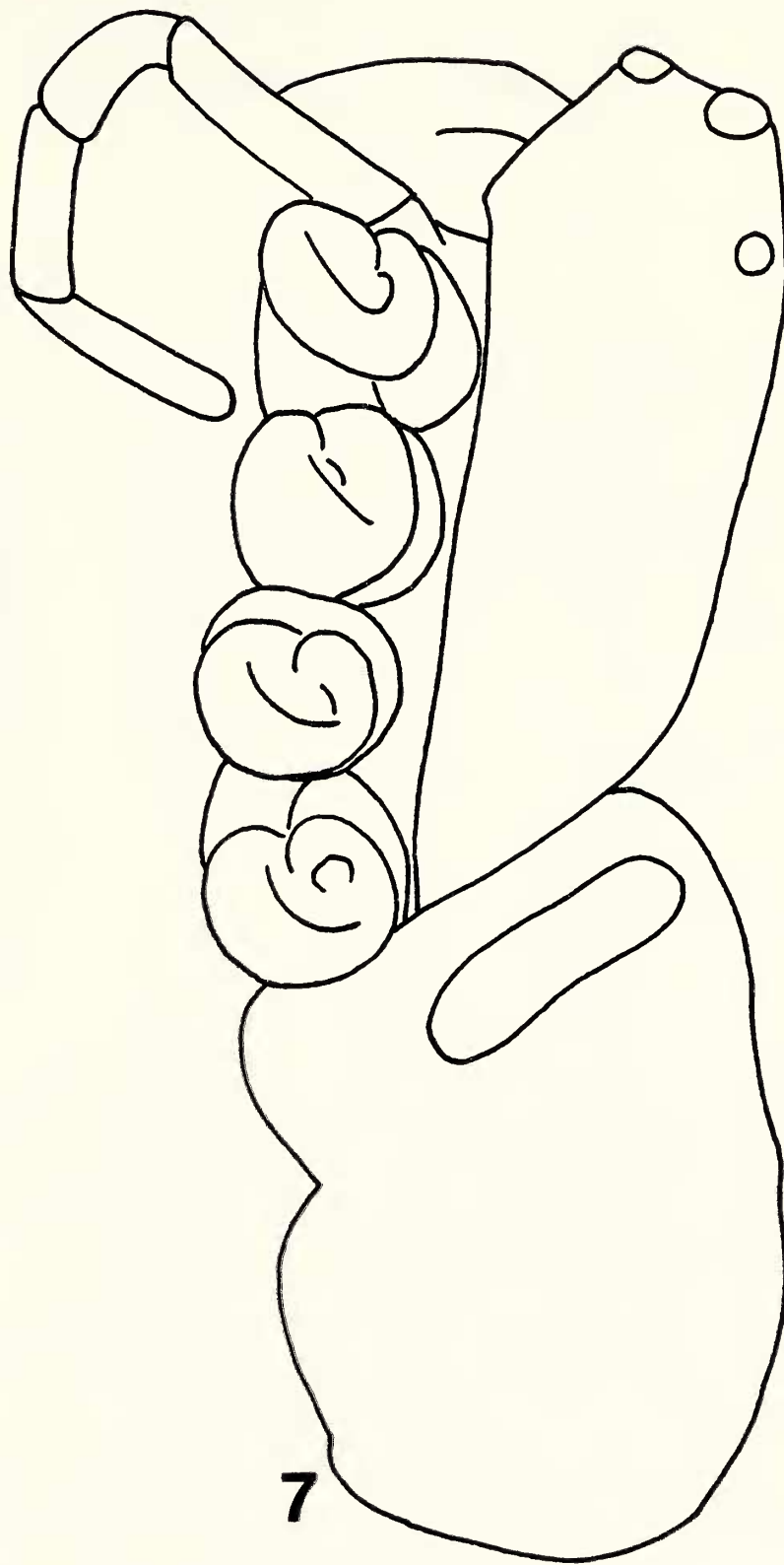
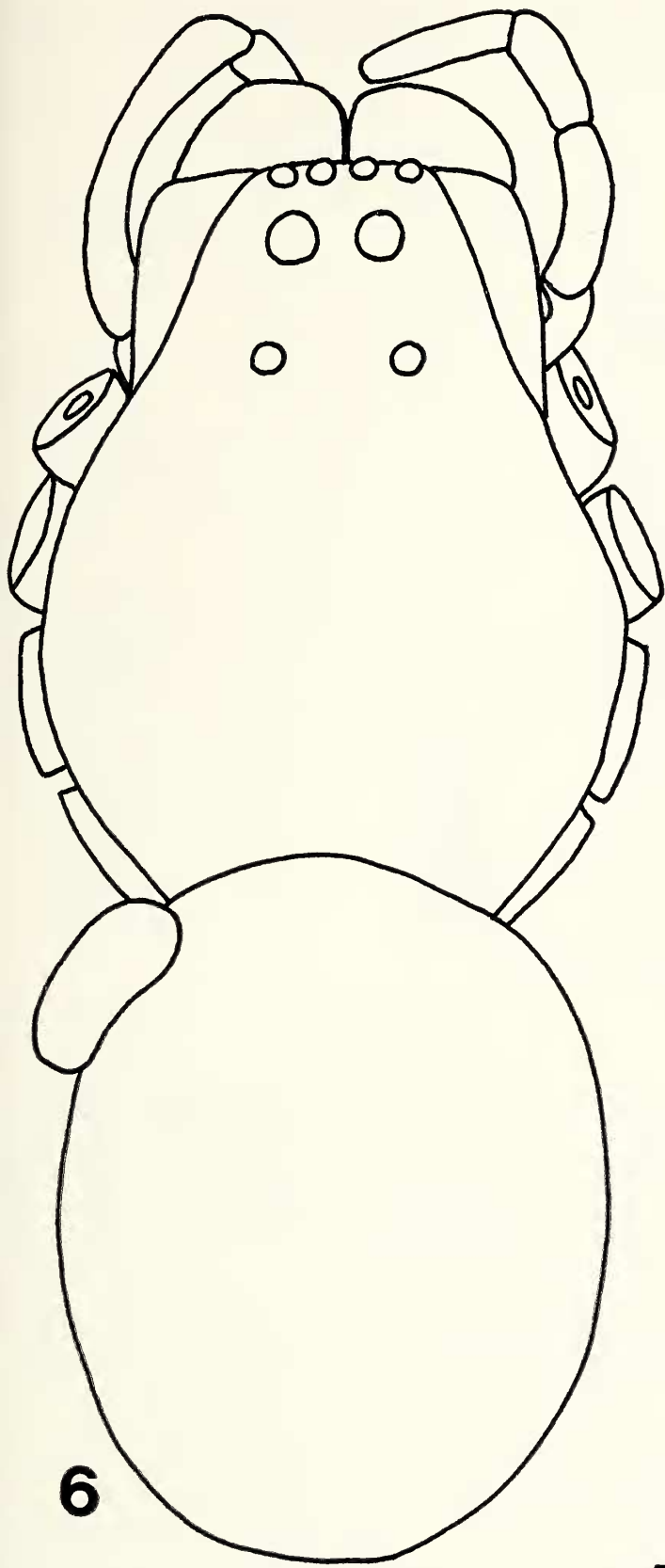
The uneaten cheliceral fangs of the prey are to be found adhering to the outside of the cocoon.

Measurements pertaining to the egg, to the larva at various stages of its existence (with reference to the site of its feeding upon the prey) and to the cocoon are given in Table III.

PARASITES AND OTHER ASSOCIATED ORGANISMS

In the sixty nests excavated during the present study remarkably few parasites and other associated organisms were present.

Two cocoons obtained from separate nests of *D. pulchricoma* at Hilton on 24.xi.1972, though similar to those of that species in general shape, appearance and size (12 mm × 6 mm), differed noticeably from them with respect to detail. Thus these two cocoons were harder, darker in colour and were constructed of a greater thickness of silk spinings, the silk thread itself being coarser. Adhering to the outside of the cocoons were the spider's cheliceral fangs,



5 mm

Fig. 6. Egg of *Dichragenia pulchricoma* (Arnold) in position on the abdomen of a lycosid spider (dorsal view).

Fig. 7. The same (lateral view).

Table III. Measurements pertaining to the egg, to the larva at various stages of its existence (with reference to the site of its feeding upon the prey), to the cocoon and to the adult of *Dichragenia pulchricoma* (Arnold).

Stage	Size range (mm.)	Number measured
Egg	1,9 × 0,6—2,3 × 0,8 (average: 2,1 × 0,7)	6
Larva feeding on spider's abdomen	2—9	7
Larva feeding on spider's cephalothorax	9,5—15	4
Larva which has completed feeding but has not commenced cocoon-spinning	15—16	2
Cocoon	9,5 × 4—12,5 × 5,5 (average: 10,8 × 4,8)	20
Adult (a) female	10—16 (average: 13,1) (74% 12—14)	39
(b) male	8—11 (average: 9,6) (81% 9—10)	21

as is the case with *pulchricoma* cocoons. One of the two cocoons, damaged in the excavation, was opened (on the date of excavation) and within was found a developing pupa with legs, wing buds and head clearly distinguishable. The second cocoon was kept in a gelatin capsule and 39 days later yielded a male *Ceropales punctulatus* Cam. (Pompilidae: Ceropalinae) which had emerged after cutting off one of the ends of the cocoon. *C. punctulatus* appears to be a common, widespread species and is represented in the Albany Museum by specimens from Mamathes (Lesotho), Kenton-on-Sea and various localities around Grahamstown. Dates of capture range from October to May. *Ceropales* species are known to be cleptoparasites on other Pompilidae but as far as can be ascertained no "host" wasp has hitherto been recorded for this species.

Five nests examined at Hilton during the period 16.xi.1972 to 1.xii.1972 were found to have been invaded for the purpose of nesting by leaf-cutting bees. In all cases the nest excavations were incomplete and consisted of a vertical shaft without any cells (Category A in Table I), surmounted by a turret that had barely attained the top of its arch. In Fig. 8 are shown, diagrammatically, the lengths of the leaf-nests constructed by these bees and their positions within the vertical shafts. A further *pulchricoma* nest, examined at Hilton during the same period, and consisting of 5 sealed cells and the beginning of a sixth cell, was found to have two disc-shaped pieces of bee-cut leaf in the vertical shaft. The bee responsible for the leaf-nest in one of the five former nests was captured, when emerging from the turret of the latter, and was identified as *Megachile (Eutricharaea) stellarum* Ckll. (Megachilidae: Apoidea). This species

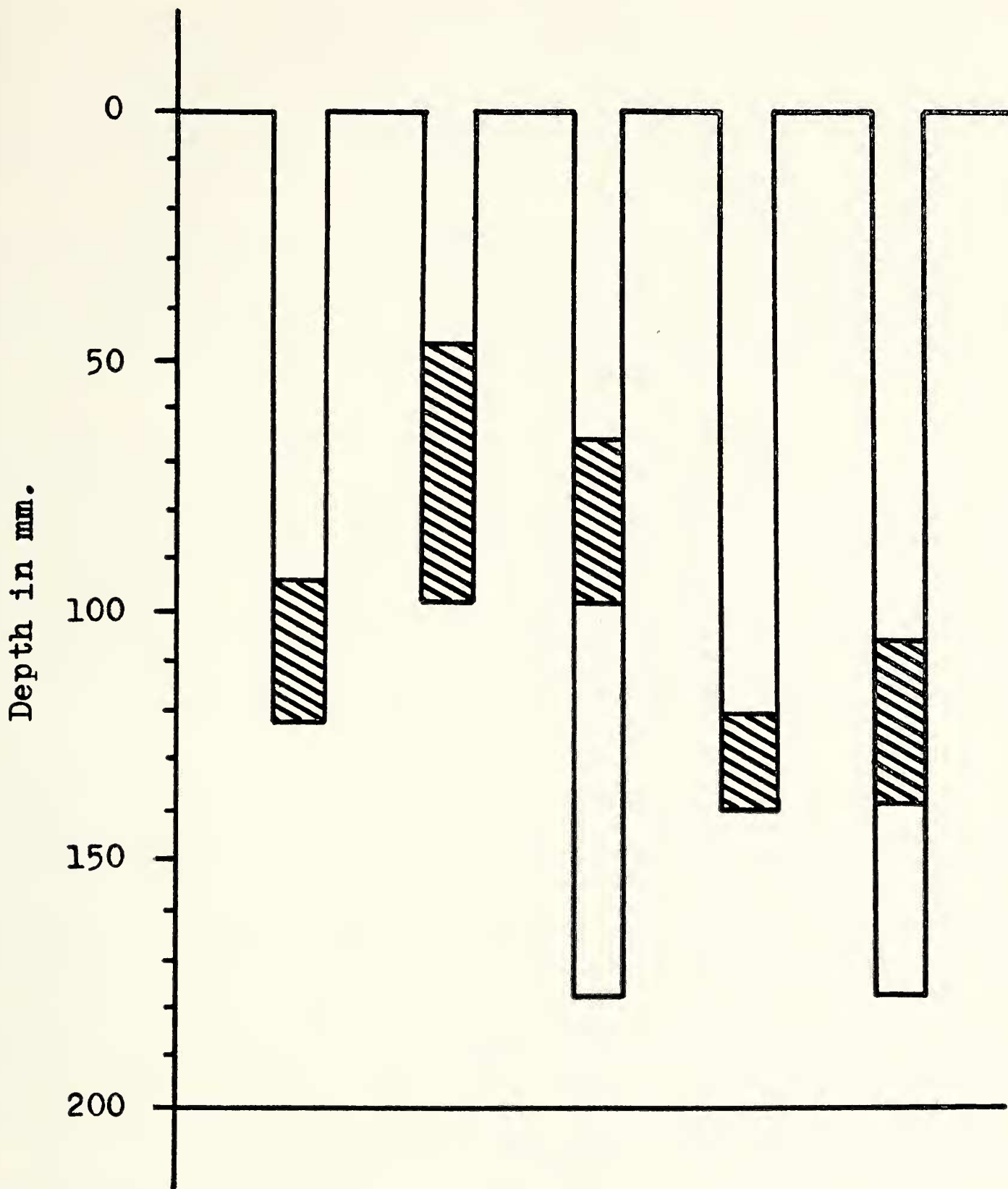


Fig. 8. Positions and lengths of megachilid leafnests within five vertical shafts of *Dichragenia pulchricoma* (Arnold).

has a wide distribution in East and South-East Africa (Pasteels, 1965:266) and is one of the most common megachilids around Grahamstown, where its flight period, as indicated by specimens in the Albany Museum collection, is from November to March. Little is known concerning its biology but it probably nests in any suitable cavity. While it is clear that in these cases *D. pulchricoma* was superseded by *M. (E.) stellarum* in its nests, it is not evident whether or not competition for the burrows arose—whether the bee ousted the rightful owner or whether it merely occupied the burrow left untenanted following its abandonment by, or the death of, the pompilid builder.

Three multicellular nests excavated at Hilton during the period 1.xii.1972 to 6.xii.1972 each included one sealed cell whose contents was overrun by pale-coloured mites. Two of these cells contained prey spiders in a very poor state of preservation on which wasp eggs or larvae could not be found; the third cell contained the rotten remains of a mature larva in its cocoon. The remains of the mature larva and of one of the prey spiders were also covered with the hyphae and the small white fruiting-bodies of a fungus.

FLOWERS VISITED BY ADULT WASPS

Adult *D. pulchricoma* of both sexes have been observed visiting flowers for the purpose of imbibing nectar. The following associations of wasps and their forage flowers have been recorded: one female on *Foeniculum vulgare* Mill. (Umbelliferae) at Belmont Valley, Grahamstown on 24.i.1970 (C. F. Jacot-Guillarmod); three males on *Maytenus linearis* (L.f.) Marais (Celastraceae) at Hilton, Grahamstown on 6.xii.1972 (F. W. & S. K. Gess); and three females on *Zizyphus mucronata* Willd. (Rhamnaceae) at the Koonap River near Adelaide (C.P.) on 20–22.xii.1972 (C. F. Jacot-Guillarmod). The flowers of all three plant species are small and inconspicuous, pale yellow or greenish-yellow in colour, with nectar, secreted on a freely exposed disc, easily accessible to short-tongued wasps such as *pulchricoma*.

DISCUSSION

The ethology of *Dichragenia pulchricoma* (Arnold) exhibits two outstanding features which mark this species as unique, firstly within its tribe, secondly within its family. Both these features pertain to the nest—to the subterranean position of the cells and to the presence of a turret rising above the burrow entrance.

As already shown, *D. pulchricoma* is, judged on morphological grounds, a member of the tribe Macromerini (= Auplopodini) of the subfamily Pepsinae, and is closely related to species of the genera *Phanagenia*, *Auplopus* and *Ageniella*, with which it has in common certain aspects of behaviour with respect to prey selection, prey mutilation and prey transport.

The four spider families (Lycosidae, Pisauridae, Sparassidae and Salticidae), species of which are, in the present paper, recorded as being the prey of *D. pulchricoma* are amongst the eleven families recorded as prey of the genera *Phanagenia*, *Auplopus* and *Ageniella* by various authors: Evans and Yoshimoto (1955:17), Kurczewski (1961:23–4), Kurczewski and Kurczewski (1968a: 6–8, and 1968b: 369), Peckham and Peckham (1898:164), Richards and Hamm (1939:73), Townes (1957:143–219) and Wasbauer and Powell (1962:395).

Amputation of the legs of their prey spiders at the coxal-trochantal joint, prior to the removal of the prey to the nest is a characteristic behavioural feature of the Macromerini and is recorded in *Phanagenia*, *Auplopus* and *Ageniella* by the above listed authors.

The method of transporting the prey to the nest practised by *D. pulchricoma* is the same as that reported for *Phanagenia* by Kurczewski (1961: 23–4), a method apparently adopted also by *Ageniella* but not by *Auplopus* (Kurczewski, 1961: 24, and 1968a: 6–8). The latter, though also straddling the prey, transports it venter up, grasped by the spinnerets and not dorsum up, grasped by the base of a chelicera, as is the case in the other genera.

Although there is a strong similarity between *D. pulchricoma* and members of the other genera in various aspects pertaining to the prey, there is a remarkable dissimilarity in the form and situation of the nest.

The Macromerini are characterized by their construction using wholly foreign materials, primarily mud, of aerial nests consisting of separate but adjacent cells. In the nature of their construction these nests parallel those built by some Eumenidae and some Stenogastrinae (Vespidae).

Among the species whose nesting is better known is the widespread North American *Phanagenia bombycina* (Cresson). An early account, based upon examination of a nest found in New Hampshire was published by the Peckhams (1898: 164—5). The nest in question was built under a stone and consisted of sixteen small mud cells about 15×8 mm. Townes (1957: 143) lists various records and confirms that "its nest of mud cells is placed usually under stones".

Concerning the very large genus *Auplopus*, Townes (1957: 145) states that probably all species nest in mud cells. Two instances of the nest-building of the North American *Auplopus architectus* (Say) were reported by the Peckhams (1898: 165—6): one set of three cells (each 8 mm long by 5 mm wide) being constructed in the folds of an undisturbed furled flag upon a porch, another set of two cells being fastened to the inside of a boat house. Concerning the same species, Townes (1957: 165) states that the cells which are made of hard clay are always "under a stone in the open, in an irregular group of usually three to five, plastered to the stone and against one another, in a place the stone happened to be raised above the soil enough to give the female space". Other North American species of *Auplopus* are recorded by Townes as building their mud cells in a variety of locations such as under logs, under loose bark or in various holes and crevices including old mud nests of species of *Sceliphron* and *Trypoxylon*. Evans and Eberhard (1970: Fig. 67) published a drawing of the nest of a Philippine species.

Among the few species of the genera *Phanagenia* and *Auplopus* whose nesting has been noted, some degree of variation in the placement of the mud cells thus occurs but in all cases the nests have been aerial. No record of subterranean nesting by a member of the Macromerini has been found in the literature available to the authors for consultation, and *D. pulchricoma* which does construct its cells in the ground thus appears to be unique within its tribe.

The form of the subterranean portion of the nest of *D. pulchricoma* seems to approximate most to the nest of the North American *Priocnemis minorata* Banks which has been closely described and figured by Yoshimoto (1954). *Priocnemis minorata* belonging to the tribe Pepsini of the subfamily Pepsinae (which includes as its other tribe the Macromerini), constructs an open nest in heavy clay-loam soil, containing from one to seven cells arranged more or less spirally in ascending order around the common vertical shaft excavated by the wasp. Several other species of the tribe Pepsini, notably *Priocnemis exaltatus* (Fabr.) in Sweden and two species of *Priocnemioides* in Chile have likewise been observed by various authors (see Evans, 1953) to construct several lateral cells from a common burrow. However, the nest of *D. pulchricoma* differs from those of these behaviourally advanced Pepsini and indeed from the nests of all other Pompilidae (at least those species whose nesting has been studied and recorded) in having the entrance to the subterranean burrow surmounted by a mud turret.

The ethology of *D. pulchricoma* thus appears to be in some respects intermediate between that of the ethologically advanced species of the tribe Pepsini (such as *P. minorata*) which construct multicellular subterranean nests and that of those Macromerini (such as *Phanagenia* and *Auplopus* species) which construct aerial mud nests. However, rather than forming a connecting link between these two ethological groups, it seems likely that the ethology of *D. pulchricoma* represents a side branch arising at this point from the main stream of the ethological evolution of the Pompilidae.

As indicated by Evans (1953) in his account of the comparative ethology of the Pompilidae, the Macromerini which build aerial nests belong to a special group arising from ground

nesting forms which like themselves belong to an advanced ethological type characterized by the fact that nest building precedes hunting, a sequence not widespread in the Pompilidae but shown by all species constructing multicellular nests. It is clear that ethologically *D. pulchricoma* shared the same origin with these other Macromerini with which, as shown, it has in common the behaviour with respect to prey selection, mutilation and transport, while at the same time retaining the more conservative nesting situation. Like them, *D. pulchricoma* is a worker in mud but, whereas *Phanagenia* and *Auplopus* species which freed themselves of the ground use this medium to build aerial cells, *D. pulchricoma* uses it to build a turret with which to surmount the burrow entrance. In this connection it is of interest that the use of the pygidium as a "trowel" for smoothing the surface of the mud structure as reported for *Auplopus* by Evans and Eberhard (1970: 100 and Fig. 67) is not seen in *D. pulchricoma* which as already stated does no smoothing of its turret walls.

Finally, it is interesting to note the similarity between the multicellular subterranean nests surmounted by mud entrance turrets as built by *Dichragenia pulchricoma* (Arnold) of the Pompilidae and those built by some Eumenidae and some Masaridae (*Ceramius* species) and that in all three families the ethological evolution with respect to the situation and form of the nest is from simple nests in the ground to free aerial mud nests, a trend paralleled also in the Sphecidae.

SUMMARY

The ethology of *Dichragenia pulchricoma* (Arnold) (Hymenoptera: Pompilidae: Macromerini) in the Eastern Cape Province of South Africa is described. Various facets of the nesting behaviour are dealt with but particular attention is given to the description of the form of the nest, which by possessing a mud entrance turret appears to represent a nest-type previously unknown within the Pompilidae. The nest situation and type as well as various aspects of behaviour relating to nest provisioning are compared with those exhibited by related genera and the position of the present species within the ethological evolution of the Pompilidae is suggested.

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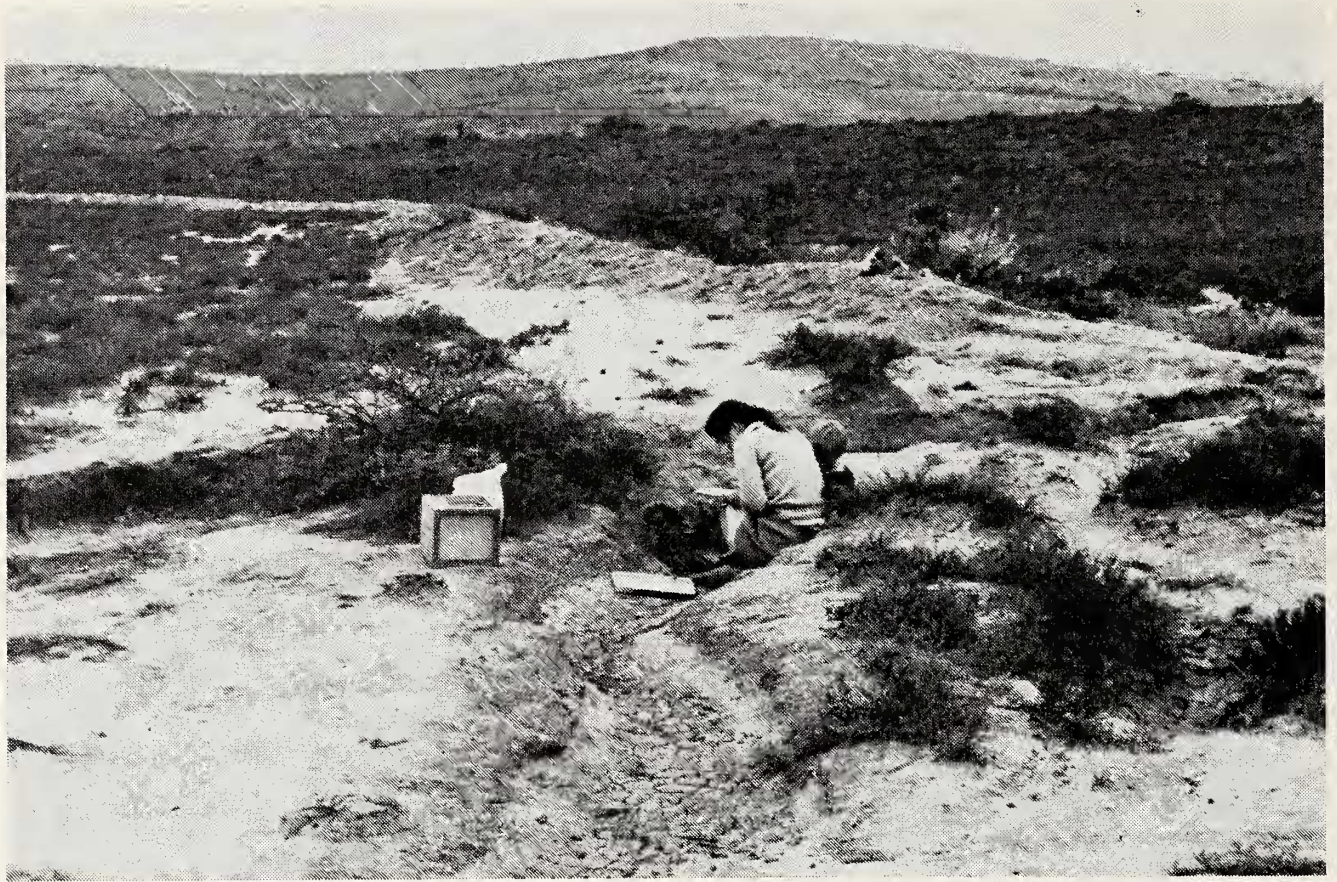


Plate 1. Hilton, 15.xi.1972. Excavation of a nest situated on the side of a small erosion gully.



Plate 2. Hilton, 1.iii.1973. Situation of a nest (marked by arrow) on raised bank of earth. Note rain water pool, sedges and grasses.



Plate 3. Hilton, 9.ii.1973. Situation of a nest (marked by spray-can in lower left corner) at a step in the ground level of an eroded area. Note rain water pool.

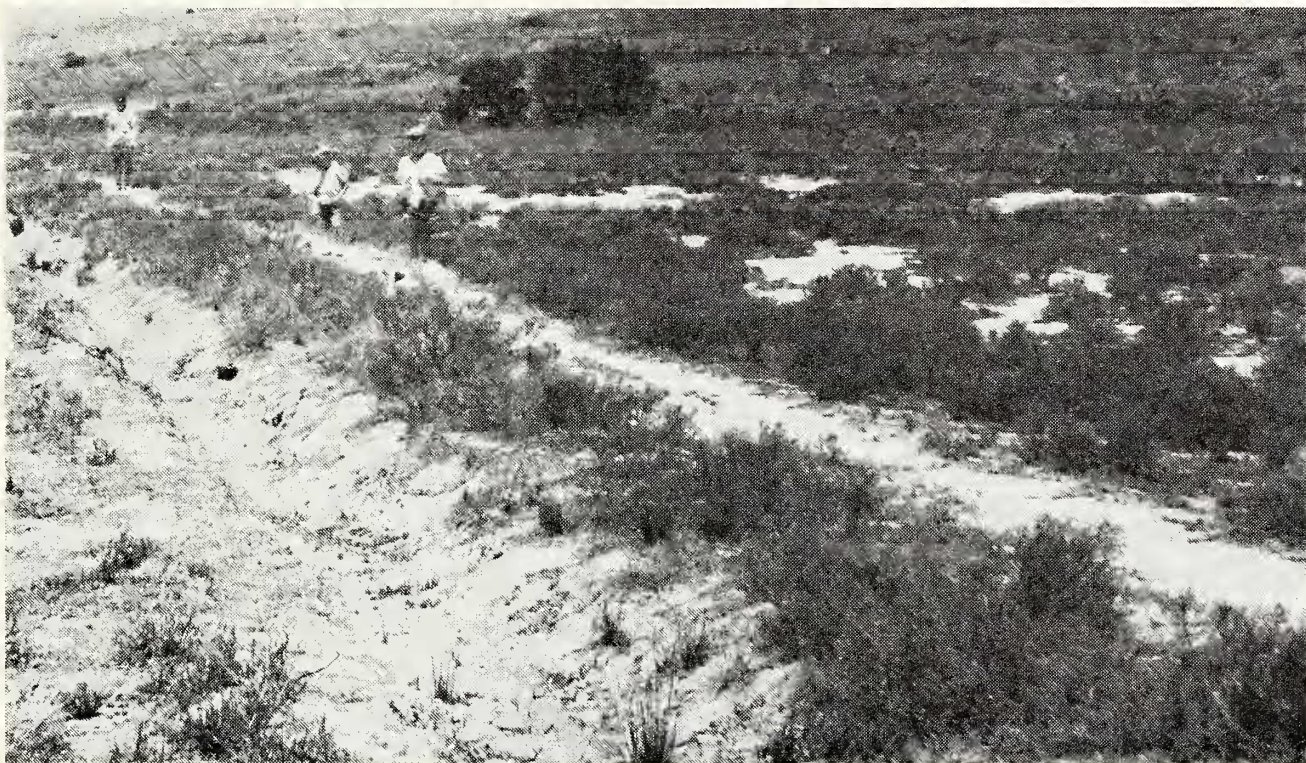


Plate 4. Hilton, 12.xi.1972. Situations of nests (marked by figures) on bare earth path running parallel to water furrow.



Plate 5. Hilton, 23.xi.1972. Newly begun turret in bare sheet-eroded area. (Burrow opening at lower right is that of an eumenid.) ($\times 1$)



Plate 6. Hilton, 23.xi.1972. Well-built turret of typical form surmounting the underground workings shown in Fig. 2. ($\times 1.2$)

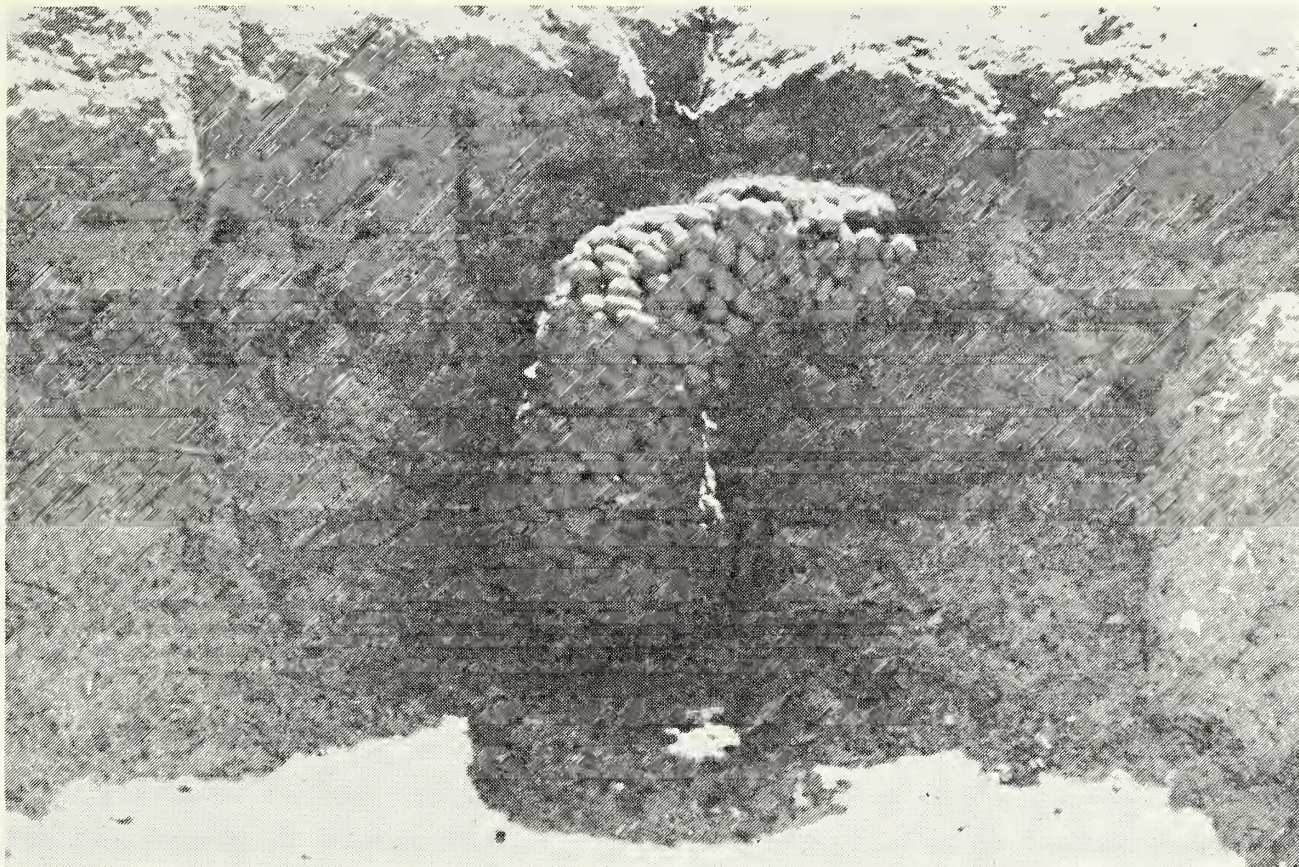


Plate 7. Hilton, 9.ii.1973. Turret of nest, the situation of which is shown in Plate 3. (x 1)



Plate 8. Hilton, 9.ii.1973. Turret of nest constructed next to base of dwarf-shrub. (x 0,7)



Plate 9. Young larva of *Dichragena pulchricoma* (Arnold) in feeding position on abdomen of a lycosid spider. ($\times 6$)